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Impact of Ozone on Vegetation

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THE IMPACT OF OZONE ON VEGETATION

by

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16. ABSTRACT Visible injury on vegetation is one of the earliest and most obvious manifestations of ozone injury. However, ozone effects are not limited to visible injury; impacts range from reduced plant growth, decreased yield, changes in crop quality and alterations in susceptibility to abiotic and biotic stresses. Several approaches have been used to estimate the ozone concentrations and exposure durations that induce foliar injury. Most of these studies used short-term exposures (less than 1 day) and measured visible injury as the response variable. In one study designed to estimate the concentrations and durations that would induce specific amounts of visible injury plants were exposed to a range of ozone concentrations and exposure durations and the data were evaluated by regression analysis. The data for several species are summarized to illustrate the range of concentrations required to induce foliar injury on sensitive, intermediate, and less sensitive species. An alternative approach for estimating ozone concentrations and exposure durations which induce foliar injury is the use of limiting value analysis. The limiting values were developed from a review of the literature and represent the lowest concentration and exposure duration reported to cause visible injury on various plant species. The analysis was based on more than 100 studies of agricultural crops and 18 studies of tree species.		
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Visible injury on vegetation is one of the earliest and most obvious manifestations of ozone injury. However, ozone effects are not limited to visible injury; impacts range from reduced plant growth, decreased yield, changes in crop quality and alterations in susceptibility to abiotic and biotic stresses. Plant foliage is the primary site of ozone impact although significant secondary effects, including reduced growth (both roots and foliage) and yield can occur.

Ozone exerts a phytotoxic effect only if a sufficient amount reaches the sensitive cellular sites within the leaf. It diffuses from the ambient air into the leaf through the stomata, which can exert some control on uptake, to the active sites within the leaf. Injury will not occur if (1) the rate of ozone uptake is low enough to enable the plant to detoxify or metabolize ozone or its metabolites; or (2) the plant is able to repair or compensate for the ozone impacts (Tingey and Taylor, 1982). This is analogous to the plant response to sulfur dioxide described by Thomas et al. (1950). Cellular disturbances that are not repaired or compensated are expressed ultimately as visible injury to the leaf or as secondary effects evident in reduced root growth and/or reduced yield of fruits or seeds.

Plant growth and yield is the end product of a series of biochemical and physiological processes related to uptake, assimilation, biosynthesis, and translocation. Sunlight drives the processes that convert carbon dioxide into organic compounds (photosynthesis) necessary for plant growth and development. In addition, the plant must extract essential mineral nutrients and water from the soil. Plant organs convert these raw materials into a wide array of compounds required for growth and yield. Any disruption or reduction in the rates of uptake, assimilation, or subsequent biochemical reactions is reflected in reduced growth and yield. Ozone would be expected to reduce

plant growth and/or yield if (1) it directly affected the plant process that was limiting growth or (2) it affected another step sufficiently so that this process became the growth limiting factor (Tingey 1977). Conversely, ozone will not limit plant growth and/or yield if the process affected by ozone is not or does not become rate limiting. This implies that not all effects of ozone on plants are reflected in growth or yield reductions. This also suggests that there are combinations of ozone concentration and exposure duration that the plant can experience which will not result in visible injury or reduced plant growth and yield. Indeed, numerous studies have demonstrated combinations of concentration and time that did not cause a significant detectable effect on the plant growth or yield.

Ozone induces a diverse range of effects on plants and plant communities. These effects are usually classified as either injury or damage. Injury encompasses all plant reactions such as reversible changes in plant metabolism (e.g., altered photosynthesis), leaf necrosis, altered plant quality, or reduced growth that does not impair yield or the intended use of the plant (Guderian, 1977). In contrast, damage or yield loss includes all effects that reduce the intended use or the value of the plant, such as a reduction in the quantity, aesthetic value, or any impairment in the intended use of the plant. For example, visible foliar injury to ornamental plants, detrimental responses in native species and reductions in fruit and grain production are all considered as damage or yield loss. Although foliar injury is not always classified as damage, its occurrence is an indication that phytotoxic concentrations of ozone are present. The occurrence of injury indicates the need for additional studies in these areas to assess the risk of ozone to vegetation and to determine if the intended use or value of the plants is being impaired.

LIMITING VALUES OF PLANT RESPONSE

Several approaches have been used to estimate the ozone concentrations and exposure durations that induce foliar injury. Most of these studies used short-term exposures (less than 1 day) and measured visible injury as the response variable. In one study designed to estimate the concentrations and durations that would induce specific amounts of visible injury, plants were exposed to a range of ozone concentrations and exposure durations and the data were evaluated by regression analysis (Heck and Tingey, 1971). The data for several species were summarized to illustrate the range of concentrations required to induce foliar injury (5 and 20%) on sensitive, intermediate, and less sensitive species (Table 1).

TABLE 1. OZONE CONCENTRATIONS FOR SHORT-TERM EXPOSURES THAT PRODUCE 5 OR 20 PERCENT INJURY TO VEGETATION GROWN UNDER SENSITIVE CONDITIONS^a

Exposure time, hr	Sensitive plants	Intermediate plants	Less Sensitive plants
0.5	0.35 to 0.50 (0.45 to 0.60)	0.55 to 0.70 (0.65 to 0.85)	≥0.70 (0.85)
1.0	0.15 to 0.25 (0.20 to 0.35)	0.25 to 0.40 (0.35 to 0.55)	≥0.40 (0.55)
2.0	0.09 to 0.15 (0.12 to 0.25)	0.15 to 0.25 (0.25 to 0.35)	≥0.30 (0.40)
4.0	0.04 to 0.09 (0.10 to 0.15)	0.10 to 0.15 (0.15 to 0.30)	≥0.25 (0.35)
8.0	0.02 to 0.04	0.07 to 0.12	≥0.20 (0.30)

^a The concentrations in parentheses are for the 20% injury level (table from U.S. Environmental Protection Agency, 1978).

An alternative approach for estimating ozone concentrations and exposure durations which induce foliar injury is the use of limiting value analysis (Jacobson, 1977). The limiting values were developed from a review of the

literature and represent the lowest concentration and exposure duration reported to cause visible injury on various plant species. The analysis was based on more than 100 studies of agricultural crops and 18 studies of tree species. The analysis yielded the following range of concentrations and exposure durations that are likely to induce foliar injury (U.S. Environmental Protection Agency, 1978):

Agricultural Crops

0.20 to 0.41 ppm for 0.5 hr

0.10 to 0.25 ppm for 1.0 hr

0.04 to 0.09 ppm for 4.0 hr

Trees and Shrubs

0.20 to 0.51 ppm for 1.0 hr

0.10 to 0.25 ppm for 2.0 hr

0.06 to 0.17 ppm for 4.0 hr

It should be emphasized that both approaches described here estimate concentrations and exposure durations that might induce visible injury, but they cannot be used to predict impacts on crop yield or intended use.

The concept of limiting values also was used to estimate the ozone concentrations and exposure durations which could potentially reduce plant growth and yield (U.S. Environmental Protection Agency, 1978). The data were analyzed and plotted in a manner similar to Jacobson's (1977) (Figure 1). In Figure 1 the line bounds mean ozone concentrations and exposure durations below which effects on plant growth and yield were not detected. This graphical analysis used data from both greenhouse and field studies and

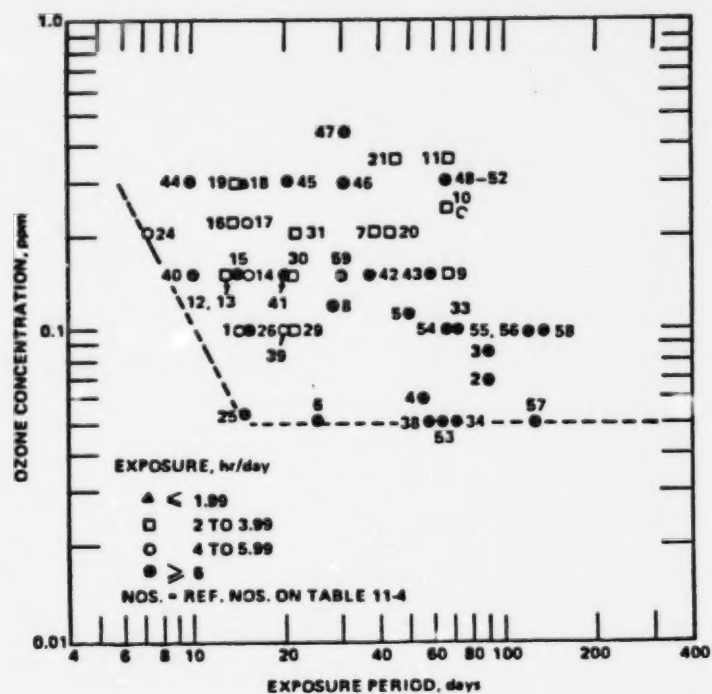


Figure 1. Relationship between ozone concentration, exposure duration, and a reduction in plant growth or yield. The numbers on the figure refer to reference numbers from Table 11-4. Source: U.S. Environmental Protection Agency, 1978 (Chapter 11).

indicates that the lower limit for reduced plant performance is a mean ozone concentration of 0.05 ppm for several hours per day for exposure periods greater than 16 days. At 10 days the ozone response threshold increases to about 0.10 ppm and 0.30 ppm at 6 days.

METHODS FOR DETERMINING OZONE YIELD LOSSES

Diverse experimental procedures have been used to study the effects of ozone on plants, ranging from studies in highly controlled conditions to exposures in open-top chambers and field exposures without chambers. In general, the more controlled conditions are most appropriate for investigating specific responses and for providing the scientific basis for interpreting and extrapolating results. These systems are powerful tools to gain increased understanding of the biological effects of air pollutants. To assess the impact of ozone on plant yield, however, it is desirable to minimize deviations from the typical environment in which the plant is grown. That is for field crops, the studies should be conducted in the field; for crops typically grown in glass houses, the studies should be conducted under glass house conditions.

In 1980 EPA initiated the National Crop Loss Assessment Network (NCLAN) to improve estimates of the magnitude of crop losses caused by ozone (Heck et al., 1982). The primary objectives of NCLAN were:

1. To define the relationships between yields of major agricultural crops and ozone exposure as required to support the needs of economic assessments and the development of National Ambient Air Quality Standards;
2. To assess national economic consequences resulting from the exposure of major agricultural crops to ozone; and

3. To advance the understanding of the cause and effect relationships that determine crop responses to pollutant exposures.

The NCLAN experimental sites were selected on the basis of (1) differing climatic conditions, (2) distribution of crop species, and (3) the existence of established research groups studying air pollution effects on plants. Cultural conditions approximate typical agronomic practices and open-top field exposure chambers are used to minimize perturbations to the plant environment during the exposure. The studies have attempted to use realistic ozone concentrations and sufficient replication to permit the development of exposure-response models. The data have been analyzed using regression approaches. The exposures are characterized by a 7-hr (e.g., 09:00 to 16:00) seasonal mean ozone concentration. This is the time period during which ozone is added to the exposure chambers.

ESTIMATES OF YIELD LOSS

Studies, frequently using open-top exposure chambers, have been conducted to estimate the impact of ozone on the yield of various crop species. These studies can be grouped into two types, depending on the experimental design and statistical methods used to analyze the data: (1) studies that developed predictive equations relating ozone exposure to plant response; and (2) studies that compared discrete treatment levels to a control. The advantage of the regression approach is that exposure-response models can be used to interpolate results between treatment levels. However, both types of experimental design provide data useful in determining the effects of ozone on plants.

Ozone was added to either charcoal-filtered or ambient air to create the range of ozone concentrations that is needed when the regression approach is

used to estimate ozone-induced yield loss. In summarizing the data, ozone-induced yield loss was derived from a comparison of the performance of the plants in charcoal-filtered air (control). Various regression techniques have been used to derive exposure-response functions. Application of regression approaches permits the estimation of the ozone impact on plant yield over the range of concentrations, not just at the treatment means, as is the case with analysis of variance methods. Examples of graphs of exposure-response equations and the data used to derive them show the fit of the various models to the experimental data (Figure 2).

Linear regression equations have been used to estimate yield loss, however for some species and cultivars there appear to be systematic deviations from the data even though the equations had high coefficients of determination (r^2). The use of plateau-linear or polynomial equations seemed to fit the data better. More recently, a Weibull model which yields a curvilinear response line seems to provide reasonable fit to the data. This model has also been used to develop yield response equations, combining the responses for several cultivars of a species (Figure 3). Statistical analysis indicated that for most crops the model fit the combined data as well as the data for the individual cultivars. Yield loss estimates for some major crop species were made using the combined models; it appears that ozone impacts the yield of corn and wheat much less than it does the yields of cotton, soybeans, and peanuts.

The yield response models can be used to estimate the ozone concentrations that induce losses (e.g., 10 and 30%) in various plant species and cultivars (Table 2). In general, when several models were fit to the data they tended to predict similar yield-reducing concentrations. In the case of corn, turnip, and winter wheat, however, the linear model tended to estimate

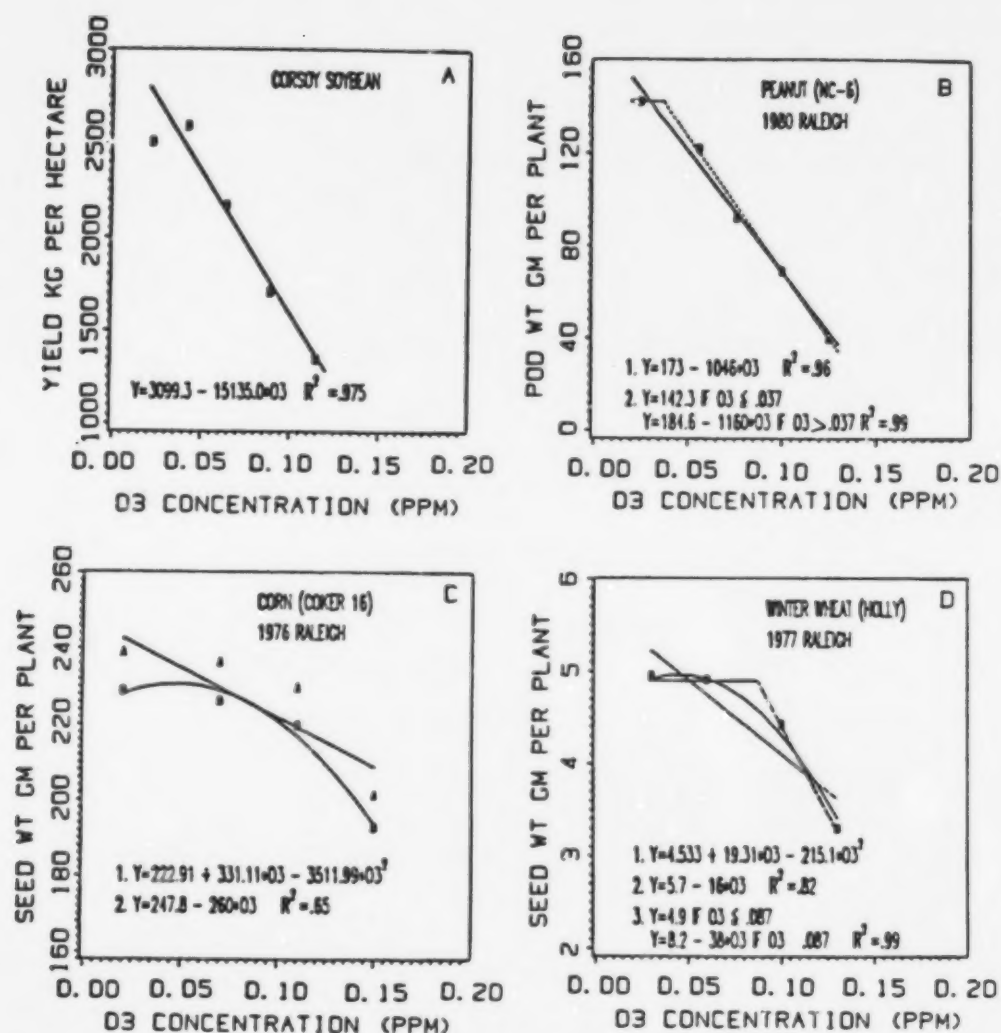


Figure 2. Examples of the effect of ozone exposure on the yield of various plants. The ozone concentration (ppm) is expressed as the 7-hr seasonal mean. Soybean (A) data from Kress and Miller (1983); peanut (B) data from Heagle et al. (1983b) and Heck et al. (1982); corn (C) and wheat (D) data from Heagle and Heck (1980) and Heck et al. (1982).

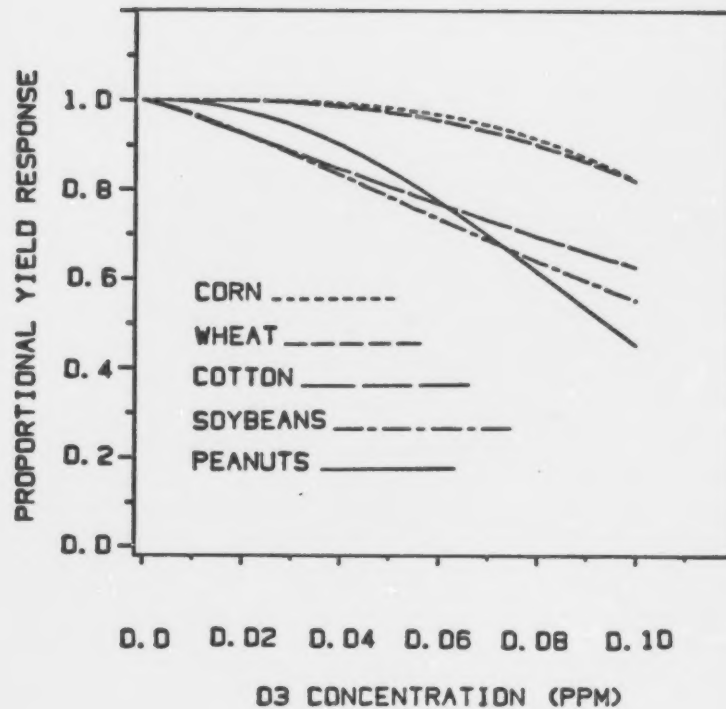


Figure 3. The relative ozone-induced yield reduction of selected crops as predicted by the Weibull model (Heck et al., 1983).

TABLE 2. SEASONAL 7-hour OZONE CONCENTRATIONS (ppm) AT WHICH YIELD LOSSES OF 10% OR 30% ARE PREDICTED FROM EXPOSURE-RESPONSE MODELS

Plants	Model	Control O ₃ Concentration	Yield Loss		Reference
			10%	30%	
Grains/Seeds					
Soybean					
(Corsoy)	kg/ha = 3099.3 - 15135 x O ₃	0.022	0.040	0.077	Kress and Miller, 1983
(Corsoy)	g/plant = 15.6 exp [-(O ₃ /0.129) ^{1.70}]	0.022	0.043	0.076	Heck et al., 1983
(Davis)	seed wt/m = 534.5 - 3988.6xO ₃ +10960x(O ₃) ²	0.025	0.038	0.070	Heagle et al., 1983
(Davis)	g/plant = 31.1 exp [-(O ₃ /0.129) ^{0.91}]	0.025	0.038	0.071	Heck et al., 1983
(Essex)	g/plant = 18.7 exp [-(O ₃ /0.309) ^{0.76}]	0.014	0.037	0.109	Heck et al., 1983
(Hodgson-F)*	g/plant = 15.2 exp [-(O ₃ /0.207) ^{0.80}]	0.017	0.039	0.096	Heck et al., 1983
(Hodgson-P)*	g/plant = 15.5 exp [-(O ₃ /0.153) ^{1.87}]	0.017	0.043	0.084	Heck et al., 1983
(Williams)	g/plant = 19.4 exp [-(O ₃ /0.243) ^{0.94}]	0.014	0.038	0.098	Heck et al., 1983
Peanut - 1979	pod wt/plant = 112 - 563 x O ₃	0.026	0.043	0.078	Heagle et al., 1983b
Peanut - 1980 ⁺	pod wt/plant = 173 - 1046 x O ₃	0.025	0.039	0.067	Heagle et al., 1983b
Peanut - 1980	pod wt/plant = 142.3 if O ₃ ≤ 0.037; if O ₃ > 0.037 PW/P = 184.6 - 1160 x O ₃	0.025	0.049	0.073	Heck et al., 1982
Peanut - 1980	g/plant = 148 exp [-(O ₃ /0.186) ^{3.20}]	0.025	0.046	0.073	Heck et al., 1983
Kidney bean	seed wt/plant = 17.44 - 35.51 x O ₃	0.025	0.072	0.165	Kohut and Laurence, 1983
Kidney bean	g/plant = 16.5 exp [-(O ₃ /0.287) ^{1.77}]	0.025	0.086	0.164	Heck et al., 1983
Field Corn					
(Coker 16)	g/plant = 247.8 - 260 x O ₃	0.02	0.113	0.300	Heck et al., 1982
(Coker 16)	g/plant = 222.91+331.11 x O ₃ - 3511.99 x O ₃ ²	0.02	0.132	-	Heagle and Heck, 1980
(Coker)	g/plant = 240 exp [-(O ₃ /0.221) ^{4.46}]	0.02	0.133	0.175	Heck et al., 1983
(PAG 397)	g/plant = 166 exp [-(O ₃ /0.160) ^{4.28}]	0.15	0.095	0.126	Heck et al., 1983
(Pioneer 3780)	g/plant = 149 exp [-(O ₃ /0.155) ^{3.11}]	0.15	0.075	0.111	Heck et al., 1983
Winter wheat					
(Blueboy II)	g/plant = 6.6 - 18 x O ₃	0.03	0.063	0.131	Heck et al., 1982
(Blueboy II)	g/plant = 5.908 + 3.958 x O ₃ - 137.7 x (O ₃) ²	0.03	0.082	0.129	Heagle and Heck, 1980
(Blueboy II)	g/plant = 5.88 exp [-(O ₃ /0.175) ^{3.22}]	0.03	0.088	0.127	Heck et al., 1983
(Coker 47-27) ⁺	g/plant = 5.8 - 21 x O ₃	0.03	0.055	0.104	Heck et al., 1982
(Coker 47-27)	g/plant = 5.765 - 18.79 x O ₃ - 20.00 x (O ₃) ²	0.03	0.055	0.103	Heagle and Heck, 1980
(Coker 47-27)	g/plant = 5.19 exp [-(O ₃ /0.171) ^{2.06}]	0.03	0.064	0.107	Heck et al., 1983
(Holly)	g/plant = 5.7 - 16 x O ₃	0.03	0.063	0.128	Heck et al., 1982
(Holly)	g/plant = 4.533 + 19.31 x O ₃ - 215.1 x (O ₃) ²	0.03	0.095	0.129	Heck et al., 1982
(Holly)	g/plant = 4.95 exp [-(O ₃ /0.156) ^{4.85}]	0.03	0.099	0.127	Heck et al., 1983
(Holly)	g/plant = 4.9 if x ≤ 0.087 if O ₃ > 0.087 g/p = 8.2 - 38 O ₃	0.03	0.100	0.126	Heck et al., 1982
(Oasis) ⁺	g/plant = 4.9 - 12 x O ₃	0.03	0.068	0.143	Heck et al., 1982
(Oasis)	g/plant = 4.475 + 3.320 x O ₃ - 93.49 x (O ₃) ²	0.03	0.088	0.138	Heagle and Heck, 1980
(Oasis)	g/plant = 4.88 exp [-(O ₃ /0.186) ^{3.20}]	0.03	0.093	0.135	Heck et al., 1983
Cotton	g/plant = 41.5 exp [-(O ₃ /0.197) ^{1.12}]	0.018	0.041	0.092	Heck et al., 1983
Root Crops					
Turnip					
(Just Right) ⁺	edible rt wt/plant = 12.9 - 94 x O ₃	0.014	0.026	0.051	Heck et al., 1982
(Just Right)	edible rt wt/plant = 10.7 if O ₃ ≤ 0.038 if O ₃ > 0.038 = 15.5 - 127 x O ₃	0.014	0.046	0.063	Heck et al., 1982
(Just Right)	g/plant = 10.89 exp [-(O ₃ /0.090) ^{3.03}]	0.014	0.043	0.064	Heck et al., 1983
(Purple Top White Globe)	edible rt wt/plant = 7.2 - 49 x O ₃	0.014	0.027	0.054	Heck et al., 1982
(Purple Top White Globe)	edible rt wt/plant = 6.0 if O ₃ ≤ 0.034 if > 0.034 ERW/P = 8.1 - 60 x O ₃	0.014	0.045	0.065	Heck et al., 1982
(Purple Top White Globe)	g/plant = 6.22 exp [-(O ₃ /0.095) ^{2.51}]	0.014	0.040	0.064	Heck et al., 1983
(Shogoin) ⁺	edible rt wt/plant = 5.3 - 36 x O ₃	0.014	0.027	0.054	Heck et al., 1982
(Shogoin)	g/plant = 4.68 exp [-(O ₃ /0.096) ^{2.12}]	0.014	0.036	0.060	Heck et al., 1983

(continued)

TABLE 2 (continued)

Plants	Model	Control O ₃ Concentration	Yield Loss		Reference
			10%	30%	
(Tokyo Cross)*	edible rt wt/plant = $18.1 - 116 \times O_3$	0.014	0.028	0.057	Heck et al., 1982
(Tokyo Cross)	edible rt wt/plant = 14.8 if $O_3 \leq 0.054$ if $O_3 > 0.054$ ERW/P = $27.0 - 226 \times O_3$	0.014	0.061	0.074	Heck et al., 1982
(Tokyo Cross)	g/plant = $15.25 \exp [-(O_3/-0.094)^{3.94}]$	0.014	0.053	0.072	Heck et al., 1983
<u>Foliage Crops</u>					
Lettuce	fresh hd wt/plant = $1065.7 - 5978 \times O_3$	0.043	0.057	0.084	Heck et al., 1982
Lettuce	g/plant = $1245 \exp [-(O_3/0.098)^{1.22}]$	0.043	0.053	0.075	Heck et al., 1983
Spinach	g/plant = $22.7 - 106 O_3$	0.024	0.043	0.081	Heck et al., 1982
(America)	if $O_3 > 0.087$ g/p = $8.2 - 38 O_3$				
(Winter Bloomsdale)	g/plant = $23.3 - 121 \times O_3$	0.024	0.041	0.075	Heck et al., 1982
(Winter Bloomsdale)	g/plant = $20.8 \exp [-(O_3/0.127)^{2.07}]$	0.024	0.049	0.080	Heck et al., 1983
(Hybrid 7)	g/plant = $42.1 - 193 \times O_3$	0.024	0.043	0.082	Heck et al., 1982
(Hybrid 7)	g/plant = $36.6 \exp [-(O_3/0.139)^{2.68}]$	0.024	0.060	0.095	Heck et al., 1983
(Viroflay)	g/plant = $46.1 - 238 \times O_3$	0.024	0.041	0.075	Heck et al., 1982
(Viroflay)	g/plant = $41.1 \exp [-(O_3/0.129)^{1.99}]$	0.024	0.048	0.080	Heck et al., 1983

* The Hodgson data were obtained from two designs in 1981; a full harvest (F) and a partial plot harvest (P), where some plants were removed prior to harvest.

* This model did not fit the data well and tended to underestimate the ozone concentrations which cause yield losses.

10 or 30% yield reductions at lower ozone concentrations than the other models. However, the similarity among the estimated concentrations for a given cultivar suggests that the predicted values are influenced to a greater extent by the original data than by the model used to describe the data. A brief review of the data (Table 2) indicates that for several species, mean yield reductions (10%) were predicted when the 7-hr seasonal mean ozone concentration exceeded 0.04 to 0.05 ppm.

In addition to studies using regression, other approaches have been used to determine if the ozone treatments were significantly different from the control. In general, these data were analyzed using analysis of variance. To summarize the data from studies that used discrete treatments, the lowest ozone concentration that significantly reduced yield was determined from the author's analysis (Table 3). The lowest concentration reported to reduce yield was frequently the lowest concentration used in the study; hence, it is not always possible to estimate a no-effect exposure level. In general, the data indicate that ozone concentrations of 0.10 ppm (frequently the lowest concentration used in the studies) for a few hours per day for several days to weeks generally caused significant yield reductions. Although it appears from this analysis that a higher ozone concentration was required to cause an effect than estimated from the regression studies, it should be noted that the concentrations derived from the regression studies were based on a 10% yield loss while in studies using analysis of variance (Table 3) the 0.10 ppm concentration frequently induced mean yield losses of 10 to 50%.

A review of several different approaches found that each approach indicated that similar ozone concentrations were phytotoxic. Data from numerous studies (summarized in U.S. Environmental Protection Agency, 1978) were used to develop limiting values which suggest that ozone concentrations

TABLE 3. OZONE CONCENTRATIONS AT WHICH SIGNIFICANT YIELD LOSSES HAVE BEEN NOTED FOR A VARIETY OF PLANT SPECIES EXPOSED TO O₃ UNDER VARIOUS EXPERIMENTAL CONDITIONS

Plant species	Exposure duration	Yield reduction, % of control	O ₃ concentration, ppm	Reference
Alfalfa	7 hr/d, 70 d	51, top dry wt	0.10	Neely et al., 1977
Alfalfa	2 hr/d, 21 d	16, top dry wt	0.10	Hoffman et al., 1975
Pasture grass	4 hr/d, 5d/wk, 5 wk	20, top dry wt	0.09	Horsman et al., 1980
Ladino clover	6 hr/d, 5 d	20, shoot dry wt	0.10	Blum et al., 1982
Soybean	6 hr/d, 133 d	55, seed wt/plant	0.10	Heagle et al., 1974
Sweet corn	6 hr/d, 64 d	45, seed wt/plant	0.10	Heagle et al., 1972
Sweet corn	3 hr/d, 3 d/wk, 8 wk	13, ear fresh wt	0.20	Oshima, 1973
Wheat	4 hr/d, 7 d	30, seed yield	0.20	Shannon and Mulchi, 1974
Radish	3 hr	33, root dry wt	0.25	Adedipe and Ormrod, 1974
Beet	2 hr/d, 38 d	40, storage root dry wt	0.20	Ogata and Maas, 1973
Potato	3 hr/d, every 2 wk, 120 d	25, tuber wt	0.20	Pell et al., 1980
Pepper	3 hr/d, 3 d/wk, 11 wk	19, fruit dry wt	0.12	Bennett et al., 1979
Cotton	3 hr/d, 2 d/wk, 13 wk	62, fiber dry wt	0.25	Oshima et al., 1979
Carnation	24 hr/d, 12 d	74, no of flower buds	0.05-0.09	Feder and Campbell, 1968
Coleus	2 hr	20, flower no.	0.20	Adedipe et al., 1972
Begonia	4 hr/d, once every 5 day for a total of 4 times	55, flower wt	0.25	Reinert and Nelson, 1979
Ponderosa pine	6 hr/d, 126 d	21, stem dry wt	0.10	Wilhour and Neely, 1977
Western white pine	6 hr/d, 126 d	9, stem dry wt	0.10	Wilhour and Neely, 1977
Loblolly pine	6 hr/d, 28 d	18, height growth	0.05	Wilhour and Neely, 1977
Pitch pine	6 hr/d, 28 d	13, height growth	0.10	Wilhour and Neely, 1977
Poplar	12 hr/d, 5 mo	+1333, leaf abscission	0.041	Wilhour and Neely, 1977
Hybrid poplar	12 hr/d, 102 d	58, height growth	0.15	Patton, 1981
Hybrid poplar	8 hr/d, 5 d/wk, 6 wk	50, shoot dry wt	0.15	Patton, 1981
Red maple	8 hr/d, 6 wk	37, height growth	0.25	Dochinger and Townsend, 1979
American sycamore	6 hr/d, 28 d	9, height growth	0.05	Kress and Skelly, 1982
Sweetgum	6 hr/d, 28 d	29, height growth	0.10	Kress and Skelly, 1982
White ash	6 hr/d, 28 d	17, total dry weight	0.15	Kress and Skelly, 1982
Green ash	6 hr/d, 28 d	24, height growth	0.10	Kress and Skelly, 1982
Willow oak	6 hr/d, 28 d	19, height growth	0.15	Kress and Skelly, 1982
Sugar maple	6 hr/d, 28 d	12, height growth	0.15	Kress and Skelly, 1982

of 0.04 to 0.06 ppm for 4 hr or more were likely to injure plant foliage. The ozone effects, summarized in Figure 1 (primarily from greenhouse studies), indicate that plant growth and yield was reduced at ozone concentrations of 0.05 to 0.08 ppm for several hours/day for several days. These concentrations are similar to the ozone concentrations shown to impact plant growth and yield in field studies (Figures 2 and 3; Tables 2 and 3) which ranged from 0.04 to 0.07 ppm.

EFFECTS ON CROP QUALITY

Although only a few studies have been reported, ozone can also reduce crop quality. Quality is a general term that includes many features of the crop such as nutritional composition, appearance, taste, and ability to withstand storage and shipment. Examples of ozone-induced alterations in quality are decreased oil in soybean seeds (Howell and Rose, 1980; Kress and Miller, 1983); decreased β -carotene, vitamin C, and carbohydrates in alfalfa (Thompson et al., 1976; Neely et al., 1977); and increased reducing sugars in potatoes, which are associated with undesirable darkening when potatoes are used to make potato chips (Pell et al., 1980).

YIELD LOSS FROM AMBIENT EXPOSURES

Of studies to determine the impact of ambient oxidants (primarily ozone) on plant yield, most have compared the yield differences between plants grown in ambient air and those grown in charcoal-filtered air. Early research documented that ambient oxidants reduced the yield and quality of citrus, grape, tobacco, cotton, and potato (U.S. Environmental Protection Agency, 1978). More recent studies have substantiated the effects of ambient oxidants on plant yield. Ozone induced significant yield reductions in tomato and bean

(MacLean and Schneider, 1976), soybean (Howell et al., 1979), two sweet corn cultivars (Thompson et al., 1976), and in native plants (forbes, grasses, and sedges) (Duchelle et al., 1983). Over several years, bean yields varied from a 5% increase to a 22% decrease in response to ozone concentrations in excess of 0.06 ppm (Heggestad and Bennett, 1981). Studies conducted on eastern white pine in the southern Appalachian mountains showed that ambient ozone has reduced the radial growth of sensitive individual trees 30 to 50% annually over the last 15 to 20 years (Mann et al., 1980; Benoit et al., 1982). Field studies in the San Bernardino National Forest showed that during the last 30 years ambient ozone reduced height growth of ponderosa pine by 25%, radial growth by 37%, and the total wood volume produced by 84% (Miller and Elderman, 1977).

STATISTICS USED TO CHARACTERIZE OZONE EXPOSURES

The characterization and representation of plant exposures to ozone has been, and continues to be, a major problem. Research has not yet clearly identified which components of the pollutant exposure cause the plant response. Most studies have characterized the exposure by the use of mean ozone concentrations although various averaging times have been used. Some studies have also used cumulative ozone dose (ppm x hr). The difficulty of selecting an appropriate statistic to characterize plant exposure has been summarized by Heagle and Heck (1980). Ambient and experimental ozone exposures have been presented as seasonal, monthly, weekly, or daily means; peak hourly means; number of hours above a selected concentration; or the number of hours above selected concentration intervals. None of these statistics adequately characterize the relationship among ozone concentration, exposure duration, interval between exposures, and plant response. The use of

a mean concentration implies that all concentrations of ozone are equally effective in causing plant responses and minimizes the contributions of the peak concentrations to the response. Most of the exposure statistics are not directly correlated and it is difficult to relate them to ambient air measurements of ozone which are usually reported as 1-hr means. Also it is difficult to transform one exposure statistic to another without re-analyzing the original air monitoring data.

A mean concentration treats low-level long-term exposures the same as high-concentration short-term ones. The use of a mean ignores the importance of peak concentrations which is inconsistent with the literature. Studies with beans and tobacco (Heck et al., 1966) showed that a dose (concentration x time) over a short period induced more injury than the same dose distributed over a longer period. Tobacco studies showed that the ozone concentration was approximately twice as important as exposure duration in causing foliar injury (Tonneijck, 1984). In beans, foliar injury occurred when the internal ozone flux exceeded $5500 \mu\text{g m}^{-2}$ in 1 hr (Bennett, 1979). A single 3-hr exposure, however, at approximately half the concentration (0.27 compared with 0.49 ppm) required a 64% greater internal flux of ozone to produce the same amount of foliar injury as the 1-hr exposure. Recent studies by Amiro et al. (1984) confirmed the non-linear relationship between ozone uptake and exposure duration required to induce visible injury. Their study also suggested the existence of a biochemical injury threshold (i.e., the ozone uptake rates that plants can experience without exhibiting visible foliar injury). The greater importance of concentration compared to exposure duration has been reported by numerous authors (e.g., Heck and Tingey, 1971; Henderson and Reinert, 1979; Reinert and Nelson, 1979).

Not only are concentration and time important but also the dynamic nature of the ozone exposure, i.e., is the exposure at a constant or variable concentration? Musselman et al. (1983) recently showed that constant concentrations of ozone caused the same types of plant responses as variable concentrations at equivalent doses. But, the variable concentration exposures caused a greater effect than the constant exposures. Growth studies with alfalfa showed that plants exposed to episodic ozone concentrations displayed greater yield losses than plants exposed to the same concentration daily, although the total ozone dose was similar between the treatments (Hogsett et al., 1985). Studies with radishes exposed to ambient ozone showed that significant yield reductions occurred when the daily maximum ozone concentration exceeded 0.06 ppm at least 10% of the days or more (Ashmore, 1984). Using stress ethylene as an indicator of ozone effects, studies with bean plants -- repetitively exposed to varying ozone concentrations and exposure durations for several days -- showed that a successive series of short episodes caused a greater plant response than a continuous exposure to the same ozone concentration for the same total exposure duration (Stan and Schicker, 1982). Studies with SO₂ also showed that plants exposed to variable concentrations exhibited a greater plant response than those exposed to a constant concentration (McLaughlin et al., 1979; Male et al., 1983).

Based on the literature and toxicological models, it appears that peak concentrations are important in eliciting plant responses. However, it should be remembered that low ozone concentrations may play an important role in predisposing the plant to subsequent episodic ozone exposures (Johnston and Heagle, 1982; Runeckles and Rosen, 1977).

RELATION BETWEEN YIELD LOSS AND FOLIAR INJURY

Because plant growth and production depend on photosynthetically functional leaves, studies have been conducted to determine the association between foliar injury and yield for species in which the foliage is not part of the yield. Some research has demonstrated significant yield loss with little or no foliar injury (e.g., Tingey et al., 1971; Tingey and Reinert, 1975; Kress and Skelly, 1982; Feder and Campbell, 1968; Adedipe et al., 1972). Other studies showed that significant foliar injury did not always cause a yield loss (Heagle et al., 1974; Oshima et al., 1975). The relative sensitivities of two potato cultivars were reversed when judged by foliar injury or yield reductions (Pell et al., 1980). In field corn, foliar injury occurred at a lower ozone concentration than yield reductions; but as the ozone concentration increased, yield was reduced to a greater extent than foliar injury was increased (Heagle et al., 1979a). In wheat, foliar injury was not a good predictor of ozone-induced yield reductions (Heagle et al., 1979b).

PHYSIOLOGICAL BASIS OF YIELD REDUCTIONS

As discussed earlier in this paper, plant growth is the cumulation of a series of biochemical and physiological processes related to uptake, assimilation, biosynthesis, and translocation. An impairment in these processes may lead to reduced plant yield if the affected process is limiting.

For growth to occur, plants must assimilate CO_2 and convert it into organic substances; an inhibition in carbon assimilation (photosynthesis) may be reflected in plant growth or yield. In several species ozone (at 0.05 ppm and greater) inhibited photosynthesis, as measured by gas-exchange (e.g., U.S. Environmental Protection Agency, 1978; Coyne and Bingham, 1978; Black et al., 1982). Biochemical studies showed that ozone (0.12 ppm for 2 hr) inhibited an

enzyme (ribulose-1,5-biphosphate carboxylase) that catalyzes the assimilation of CO₂ (Pell and Pearson, 1983).

Ozone, in addition to decreasing the total amount of CO₂ that is assimilated, alters the pattern by which the reduced amount of assimilate is partitioned throughout the plant. There is generally less photosynthate translocated to the roots and to the reproductive organs (e.g., Tingey et al., 1971; Jacobson, 1982; Oshima et al., 1978, 1979; Bennett et al., 1979). This reduces root size and vigor as well as marketable yield.

Reproductive capacity (flowering and seed set) is reduced by ozone in ornamental plants, soybean, corn, wheat, and some other plants (Adedipe et al., 1972a, Feder and Campbell, 1968; Heagle et al., 1972, 1974; Shannon and Mulchi, 1974). These data suggest that ozone impairs the fertilization process in plants. This suggestion has been confirmed in tobacco and corn studies using low concentrations (0.05 to 0.06 ppm) of ozone (Feder, 1968; Mumford et al., 1972).

Ozone both in the field and chamber studies stimulates premature senescence and leaf drop (Menser and Street, 1962; Heagle et al., 1974; Heggstad, 1973; Pell et al., 1980; Hofstra et al., 1978). In part, the ozone-induced yield reductions have been attributed to premature senescence. The premature leaf drop and senescence decrease the amount of photosynthate that a leaf can contribute to plant growth and yield and also the length or time during which the leaf contributes.

FACTORS AFFECTING PLANT RESPONSE TO OZONE

Numerous factors influence the type and magnitude of plant response to ozone. Most studies of these factors have been limited to effects on foliar injury although some have measured yield; the physiological basis for the

influences has also received some study. The factors studied include environmental, biological, and interactions with other air pollutants.

Environmental conditions. Environmental conditions before and during plant exposure are more influential in determining the magnitude of the plant response than are post-exposure conditions. The influence of environmental factors has been studied primarily under controlled conditions but field observations have substantiated the results. Most studies have evaluated the influence of only a single environmental factor and they used primarily foliar injury as the plant response measure. Some generalizations of the influence of environmental factors can be made.

1. Light conditions that are conducive to stomatal opening appear to enhance ozone injury (U.S. Environmental Protection Agency, 1978). Light is required to induce stomatal opening permitting the plant to absorb pollutants.
2. No consistent pattern relating temperature to plant response has been observed (U.S. Environmental Protection Agency, 1978), although plants do not appear to be sensitive at extremely high or low temperatures.
3. Plant injury tends to increase with increasing relative humidity (U.S. Environmental Protection Agency, 1978). The relative humidity effect appears to be related to stomatal aperture, which tends to increase with increasing relative humidity. McLaughlin and Taylor (1980) demonstrated that plants absorb significantly more ozone at high humidity than at low humidity. It is generally accepted that plants in the eastern United States are injured by lower concentrations of ozone than are their counterparts in California. This variance has been attributed to differences in humidity (U.S. Environmental Protection Agency, 1978).

4. As soil moisture decreases, plant water stress increases and there is a reduction in plant sensitivity to ozone (U.S. Environmental Protection Agency, 1978). The reduced ozone sensitivity is apparently related to stomatal closure which reduces ozone uptake (U.S. Environmental Protection Agency; Olszyk and Tibbits, 1981; Tingey et al., 1982). Water stress does not confer a permanent tolerance to O_3 ; once the water stress is alleviated the plants regain their sensitivity to O_3 (Tingey et al., 1982).

Interaction with plant diseases. Ozone affects the development of disease in plant populations. Most laboratory evidence suggests that ozone (at ambient concentrations or greater for 4 or more hours) inhibits infection by pathogens and subsequent disease development (Laurence, 1981; Heagle 1982; U.S. Environmental Protection Agency, 1978). However, increases in diseases from "stress pathogens" have been noted. For example, plants exposed to ozone were more readily injured by *Botrytis* than plants not exposed to ozone (Manning et al., 1970a,b; Wukasz and Hofstra 1977a,b; Biseassar, 1982). Both field and laboratory studies have confirmed that the roots and cut stumps of ozone-injured ponderosa and Jeffrey pines are more readily colonized by a root rot (*Heterobasidion annosum*). The degree of infection was correlated with the foliar injury (James et al., 1980; Miller et al., 1982). Studies in the San Bernardino National Forest showed that ozone-injured trees were predisposed to attack by bark beetles and that fewer bark beetles were required to kill an ozone-injured tree (Miller et al., 1982).

Interaction of ozone with other air pollutants. The report of Menser and Heggstad (1966) provided the initial impetus for studying the interaction of

ozone with sulfur dioxide. They showed that Bel W-3 tobacco plants exposed to ozone (0.03 ppm) or sulfur dioxide (0.24 to 0.28 ppm) were uninjured but that substantial foliar injury resulted when the plants were exposed to both gases simultaneously. Subsequent studies (both greenhouse and field) have confirmed and extended the observation that combinations of ozone and sulfur dioxide frequently cause more visible injury than expected based on the injury from the individual gases. This injury enhancement (synergism) is most common at low concentrations of each gas and also when the amount of foliar injury induced by each gas, individually, is small. At higher concentrations or when extensive injury occurs the effect of the individual gases tends to be less than additive (antagonistic). In addition to foliar injury, the effect of pollutant combinations has also been investigated in relation to other plant effects and these have been discussed in several reviews and numerous individual reports (e.g., Reinert et al., 1975; Ormrod, 1982; Jacobson and Colavito, 1976; Heagle and Johnston, 1979; Olszyk and Tibbitts, 1981).

There have been fewer studies of the effects of ozone and sulfur dioxide on plant yield than on visible injury (Flagler and Younger, 1982; Foster et al., 1983; Heggestad and Bennett, 1981; Heagle et al., 1983a). In field studies, the addition of sulfur dioxide to ozone generally did not influence the ozone response unless the concentrations and exposure frequencies were greater than typically occur for sulfur dioxide in the ambient air of the United States.

The applicability of the yield results from pollutant combination studies to ambient conditions is not known. An analysis of ambient air monitoring data indicated that at sites where the two pollutants were co-monitored, 10 or fewer periods of co-occurrence occurred during the growing season (Lefohn and Tingey, 1984). Co-occurrence was defined as the simultaneous occurrence of

hourly averaged concentrations of 0.05 ppm or greater for both pollutants. At this time, it appears that most of the studies of the effects on pollutant combinations on plant yield have used a higher frequency of exposure duration and pollutant co-occurrence than occurs in the ambient air.

ECONOMIC ASSESSMENT OF OZONE EFFECTS

Ozone has been identified as the most important air pollutant in terms of spatial distribution and impacts on agricultural yields. With the importance of United States agriculture to both domestic and world consumption of food and fiber, significant reduction in their supply would have substantial economic consequences. Various methods have been used to assess the economic impact of ozone, many of which have been simplistic. Reliable assessment procedures should use theoretically justified economic methodologies which consider the effects to both the producer and consumer. These methods usually address price changes due to adjustments in production and the role of the producer input and output substitution strategies. The resulting estimates more accurately assess the true economic impact than other procedures.

Numerous studies have attempted to assess the dollar losses to crop production resulting from ambient ozone. The quality of these various estimates is variable. For example, the earlier economic loss data (U.S. Environmental Protection Agency, 1978) frequently used simplistic traditional approaches which were not theoretically sound. Thus those previous estimates should be viewed with caution. Most of the recent economic assessments of agricultural losses (since 1978) have focused on regional losses. Crop loss estimates for southern California ranged from 45 (Adams et al., 1982) to approximately 100 million dollars (Leung et al., 1982). These studies used different assessment methodologies and considered the effects on different

crops. The economic impact of ozone on corn, wheat, and soybeans for the "Corn Belt" was estimated at 688 million dollars (Adams and McCarl, 1984), while for Illinois alone the losses were estimated at 55 to 200 million dollars (Mjelde et al., 1984).

Only a few studies have attempted to assess the national economic consequences of ambient ozone. The economic losses have been estimated between approximately 2 (Adams and Crocker, 1982b) and 3 billion dollars (Shriner et al., 1982). Although these estimates include more complete dose-response information for more major commodities and better air quality data than previous national estimates (U.S. Environmental Protection Agency, 1978), they should be considered preliminary, because of limited data.

It is apparent that the current dollar estimates of crop damage are useful primarily as indicators of the magnitudes of impact. A full accounting of the economic mechanisms underlying agricultural production is required to provide definitive estimates of the extent of agricultural losses. Such accounting should include both annual and perennial crops (agronomic and horticultural) and the associated dynamic adjustments of agricultural production. It must consider the effects on intermediate consumers (such as livestock growers and food processors) and final consumers (both domestic and foreign). The effect of ozone on ornamentals, both physically and economically, has also not been addressed.

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